Late summer phytoplankton blooms in the changing polar environment of the Kongsfjorden (Svalbard, Arctic)

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Abstract – Kongsfjorden (Spitsbergen, Svalbard) is an inlet treated as a model site for studies on the impact of climate change in the Arctic due to its hydrological features. In this research, seven-days monitoring was carried out to evaluate the effects of hydrological variability on phytoplankton biomass and diversity in the late summer period. Temperature, salinity, nutrients, total suspended matter, phytoplankton abundance and biomass were determined for each sample. The thermo-haline properties of the column water seemed to affect phytoplankton communities. Their abundances and biomass were correlated with the amount of the total suspended matter. Moreover, species composition and biomass dramatically changed throughout the study period. Cold-water and Atlantic species were replaced by temperate warm water dinoflagellates, including harmful species. An increase in phytoplankton biomass as well as the presence of dinoflagellate aggregations, mainly composed of *Prorocentrum* cf. *gracile*, were detected. This kind of algal accumulation is a new phenomenon in the Arctic and was probably related to the mobilization of sediment-rich glacial meltwaters. These findings, even if preliminary, suggest the need to study how additional biomass pulses and the increase of harmful species may alter the food web structure and the biogeochemical cycles, leading to major ecosystem changes.

Bloom / climate change / harmful algae / phytoplankton / Arctic fjord

INTRODUCTION

At the high-latitude ecosystems the effects of the climate changes are particularly pronounced

(Wassmann *et al.,* 2011), as they seem to affect productivity, biodiversity and phenology (timing variability) of natural communities, phytoplankton included (Ji *et al.,* 2010). By considering the critical role of these microorganisms in ocean, biological and atmospheric processes, the comprehension of the climate changes effects on phytoplankton is important to predict how these phenomena will affect life on Earth in the future (Kubiszyn *et al.*, 2014). During the last decade in the Arctic, the unprecedented reduction of the sea ice extent and thickness is exposing a growing sea surface area to solar radiation, and an increase of the phytoplankton production is observed (Arrigo & van Dijken, 2015). On the other hand, glaciers melting produces a large amount of mineral suspensoids, which reduce the availability of photosynthetically active radiation (PAR) and ultraviolet radiation (UVR) and increase the supply of inorganic and organic nutrients. These contrasting effects influence not only the autotrophic productivity, but also its diversity (Sommaruga, 2015), as the answer to the changed environmental conditions are different among phytoplankton types (Li *et al.,* 2009). Smaller phytoplankton (namely picophytoplankton, size < 2 µm) seem to be favoured in the new global warming conditions, due to their capacity to assimilate nutrients and light as well as to resist to sinking (Li *et al.,* 2009). Long-term analysis of satellite data are providing new insights into the effects of climate change on the timing of phytoplankton blooms. Usually phytoplankton growth season began in April and ended in September, but recently the summer Arctic blooms have been detected an average of 50 days earlier than 14 years ago (Kahru *et al.,* 2011). Blooms of pico- and nano-sized phytoplankton as well as shifts in phytoplankton bloom timing could have important implications for the higher trophic levels, particularly for the zooplankton grazers (Ji *et al.,* 2013).

The knowledge of Arctic biodiversity is advocated for the protection and conservation of this ecosystem and international agreements (e.g. Convention on Biological Diversity) have been launched. Unfortunately, phytoplankton communities are poorly considered in these initiatives, despite their role in the functioning of the ecosystems (Poulin *et al.,* 2011).

Kongsfjorden's marine ecosystem has been extensively investigated for many years and it has been treated as a model site for studies on the impact of climate change in the Arctic (Hop *et al.,* 2002). The fjord is influenced by the Atlantic water inflow and by the tidal glaciers melting: both the effects are expected to become stronger in the future (Hop *et al.,* 2002). The planktonic communities are likely to be very sensitive to these effects (Keck *et al.,* 1999; Wiktor & Wojciechowska, 2005; Mc Laughlin & Carmack, 2010; Sommaruga, 2015). Mixing of Atlantic waters with glacial freshwater and enhanced sediment concentration are important determinants for phytoplankton growth and species composition in the fjord (Hasle & von Quillfeldt, 1996; Piquet *et al.,* 2010). Biological investigation and phytoplankton studies (Halldal & Halldal, 1973) revealed a phytoplankton

community characterized by an annual peak in spring due to diatoms and prymnesiophyceae (*Phaeocystis pouchetii* (Hariot) Lagerheim). In summer phytoplankton assemblages were dominated by small-sized species (mainly phyoflagellates), and characterized by low abundances and high diversity (Eilertsen *et al.*, 1989; Hop *et al.*, 2002; Wiktor &Wojciechowska, 2005; Seuthe *et al.*, 2011). Recently, the recorded decrease of diatoms and the increase of nano-sized flagellates has been considered as a possible effect of the changing Atlantic water inflow in the fjord (Piwosz *et al.*, 2009; Hegseth & Tverberg, 2013; Kubiszyn *et al.*, 2014). Only recently, the effects of meltwaters turbidity on phytoplankton productivity and diversity have begun to be studied, and for coastal sites (Sommaruga, 2015), including the Kongsfjorden, few data are available.

By considering all these aspects, the aim of this paper was to analyse phytoplankton biomass and diversity in relation to the hydrological features of the Kongsfjorden, during a survey carried out in September 2013 at five coastal stations of Kongsfjorden. In particular, one of these stations (MDI station) had been sampled for seven days to evaluate the effects of changing hydrological regime and on the effects of melting waters on the phytoplankton communities.

MATERIAL AND METHODS

Study area

Kongsfjorden (Fig. 1), located off the northwestern coast of Svalbard (79°N, 12°E), shares a common mouth with the adjacent shelf, where the water masses are a mixture of warm, saline Atlantic water and the colder, fresher Arctic water (Wang et al., 2009). Relatively warm Atlantic water is carried in the fjord by the West Spitsbergen current (WSC) at irregular intervals where it mixes with colder water (Cottier et al., 2005). Mooring monitoring since 2001 revealed the seasonal and annual variability in the heat content and in the timing and duration of the advective period of the Atlantic inflow, giving rise to warm and cold years (Cottier et al., 2005).

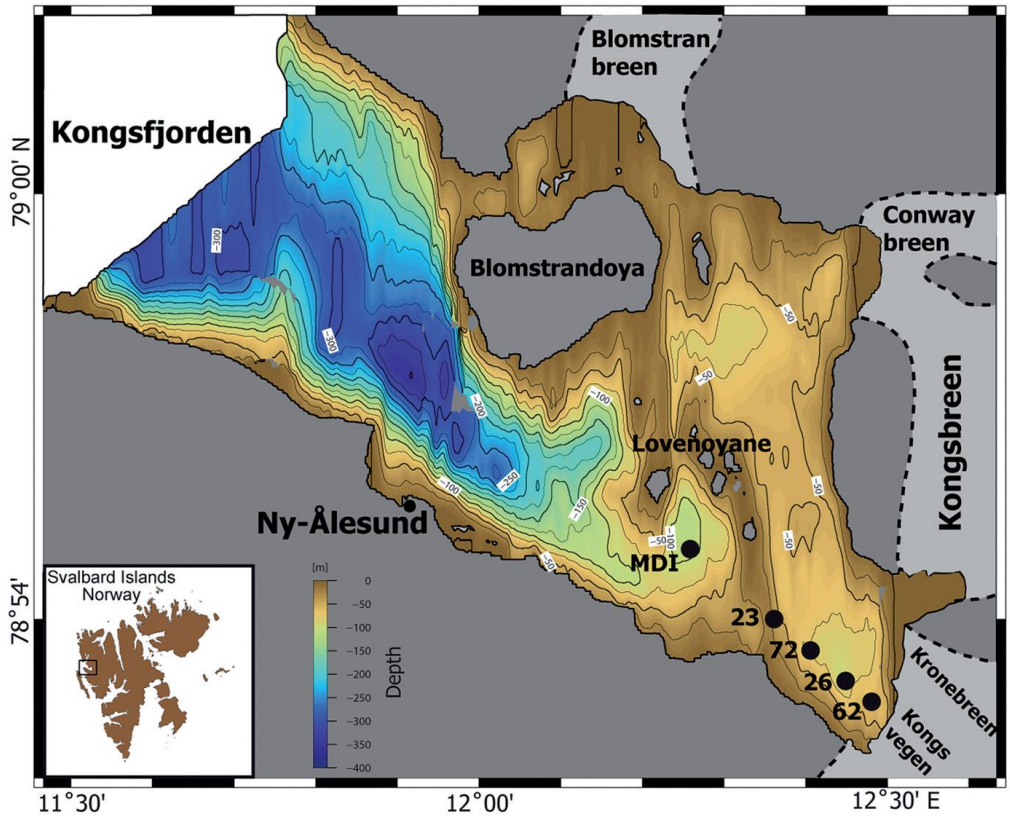


Fig. 1. Map of the Kongsfjorden with the sampling stations.

In summer, Kongsfjorden undergoes an intense and rapid shift from an Arctic water to an Atlantic water dominated system (Hop et al., 2002), and the fjord receives large quantities of freshwater from glacier melting. Reddish sandstone has been found near this glacier, and in summer, some rivers are strongly discoloured by meltwater. Discharge of freshwater and sediments by the rivers into the fjord results in i) a patchy discoloration of the surface layer; ii) a salinity gradient in horizontal as well as vertical direction; iii) a reduced transparency of the stabilized surface layer (Hasle & Heimdal 1998). Wet precipitation data collected from 29th August to 10th September showed that it was raining from 4th to 8th September, and the maximum (3.3 mm d–1) was registered on 5th September (Fig. 2). Precipitation data have been obtained by the eKlima database, managed by the Norwegian Meteorological Institute (eklima.no)

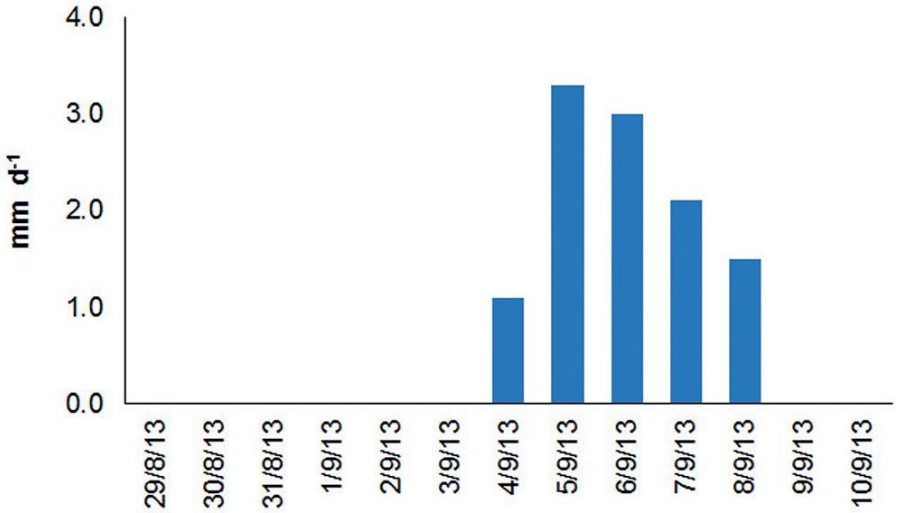


Fig. 2. Wet precipitation data (mm d–1) collected from 29th August to 10th September 2013 at Kongsfjorden. Data furnished by the Norwegian Meteorological Institute (eklima.no).

Sample collection and abiotic factors

Samplings were carried out from 5th to 11th September 2013 at the MDI station and 6th September in a transect (four stations: 23, 72, 26, 62) from MDI station to glaciers (Fig. 1; Table 1). At the MDI station, the samples have been named according to the dates of sampling as follows: MD05, MD06, MD09, MD10 and MD11.

For each sampling, temperature and conductivity were recorded along the water column with a SeaBird Electronics SBE-16 plus CTD profiler. Samples were collected by using a 10-L Niskin bottle to determine nutrients ($N\text{-}NO_3^-$, $N\text{-}NO_2^-$, $N\text{-}NH_4+$ and $P\text{-}PO_4^{3-}$), Total Suspended Matter (TSM) and phytoplankton abundance and biomass.

Table 1. Localization of the sampling stations and depths investigated in the Kongsfjorden

Date	*Station*	*Longitude*	*Latitude*	*Depth (m)*	*Samplings (m)*
5-11 September	MDI	78° 54.859‘ N	12° 15.411’ E	~ 102	0, 5, 25, 50, 75, 100
6 September	23	78° 53.757’ N	12° 22.594’ E	36	0
6 September	72	78° 52.466’ N	12° 30.960’ E	70	0
6 September	26	78° 52.881’ N	12° 29.069’ E	74	0
6 September	62	78° 53 359’ N	12° 25.473’ E	81	0

Samplings were carried out at the MDI station at surface, 5 m, 25 m, 50 m, 75 m, 100 m depths, and while at the other four stations only at the surface layer.

Samples for nutrient determinations were filtered using GF⁄F glass-fibre filters and kept frozen (–20 °C). Analytical determinations were performed according to Strickland & Parsons (1972), and N-NH4+ was measured according to Aminot & Chaussepied's method (1983). All nutrient concentrations were determined using a Varian Mod. Cary 50 spectrophotometer. To calculate the total suspended matter (TSM, mg l−1), water samples were filtered on pre-weighed and pre-combusted GF/F filters, rinsed with MilliQ water, oven-dried (50°C), and then weighed.
Daily trends of abiotic factors along the water column (0-100 m) were reported as weighted mean values.

Phytoplankton counting and Carbon content evaluation

Phytoplankton samples, freshly collected, were fixed with Lugol's iodine solution and examined by an inverted microscope (Axiovert 200M zeiss) equipped with phase contrast at a magnification of 200×, 400× and 630×. Depending on phytoplankton densities, sub-samples, varying from 50 to 100 ml, were allowed to settle for 24-48 hours and examined following the Utermöhl method (Utermöhl, 1958). Cell counts were performed along transects (1-4) or in random fields (30-60); in addition, half of the Utermöhl chamber was examined to obtain a more correct evaluation of less abundant phytoplankton taxa. Nanophytoplankton (2-20 µm) were counted in 15 randomly selected fields (zingone et al., 2010).
The water samples containing the algal aggregates were analysed by using a modified version of the method described by Totti et al. (2004) for counting the microphytobenthos of soft substrates. One milliliter of sample was diluted with 9 ml of filtered seawater and stirred for time necessary to make it homogeneous. A subsample of 1 ml was gently poured into the sedimentation cylinder (10 ml) filled with filtered seawater and allowed to settle for at least 10 hours. Then, the chamber was observed at the inverted microscope and counting was performed in the same manner reported for disaggregated samples.
The cell biovolumes were measured approximating species shapes to geometrical models (Hillebrand et al., 1999). The carbon content was calculated from mean cell biovolumes using the formula introduced by Menden-Deuer & Lessard (2000).

Conventional and confocal microscopy

Microalgae were examined under light microscopy (Axiovert 200M Zeiss) equipped with phase contrast at a magnification of 400× and 630× for taxonomical analysis. The thecal plate morphology

of Alexandrium species was examined using UV epifluorescence microscopy after Calcofluor staining (Fritz & Triemer, 1985) under an Axioskop zeiss microscope. Images were acquired with a Canon Power Shot G5 digital camera. Samples were also observed by a laser scanning confocal microscope (LSM 710 zeiss). Chlorophyll epifluorescence was detected with the TRITC filter set (> 650 nm). Images were processed using Adobe Photoshop 7.0 software (Mountain View, CA, USA).

Statistical analyses

Statistical analyses were performed to evaluate the relationships between phytoplankton (abundances and biomass) and the environmental variables. Phytoplankton data were log-transformed. Statistics was carried out using the computer package STATISTICA Version 7.0.

RESULTS

Abiotic variables

At the surface layer, a high suspended particle load gave a reddish-brown colour to the water. Due to this evidence, the underwater PAR (E^+_0) attenuated quickly in the upper water column and at the 5 m depth a low irradiance (~0.7% E^+_0) was detected.

Temperature increased from surface to 50 m depth (maximum 6.2°C) and then decreased to the bottom, where the minimum value (3.3°C) was monitored. Salinity generally increased with depth from surface (minimum value 29.7) to the bottom (maximum value 34.9). Thermo-haline properties observed at the MDI station revealed the presence of three main water masses (Fig. 3): i) a superficial, of internal origin to the fjord, characterised by T > 3°C and S < 34 (Surface Water; SW); ii) a deep, of external origin to the fjord, defined as T > 3°C, S > 34.65 and density < 27.92 (Atlantic Water; AW); iii) an intermediate, of mixed origin, defined as T > 5°C and S from 34.00 to 34.65 (Intermediate Water, IW). The extension of Intermediate Water, unexpectedly strongly changed within a week of sampling, with clear implications also on the extension of Surface and Atlantic waters.

In Fig. 4 are reported the weighed mean (0, 5, 25, 50, 75, 100 m) values of nutrient concentrations, N:P ratio and TSM. Nutrient concentrations did not change significantly over time, except for $N\text{-}NO_3^-$, which reached its highest value the last sampling day (MD11). $N\text{-}NH_4^+$ values varied from 0.81 to 1.51 mM m^{-3}, $N\text{-}NO_2^-$ from 0.05 to 0.13 mM m^{-3} and $N\text{-}NO_3^-$ from 0.38 to 1.95 mM m^{-3}. $P\text{-}PO_4^{3-}$ concentrations ranged between 0.55 to 0.74 mM m^{-3}. The highest concentrations of $N\text{--}NO_2^-$, N-

NO_3^- and $P\text{-}PO_4^{3-}$ were detected at the deeper waters. On the contrary, $N\text{-}NH_4^+$ concentrations reached the highest values at the surface waters. N:P ratio ranged between 2.45 to 4.84.

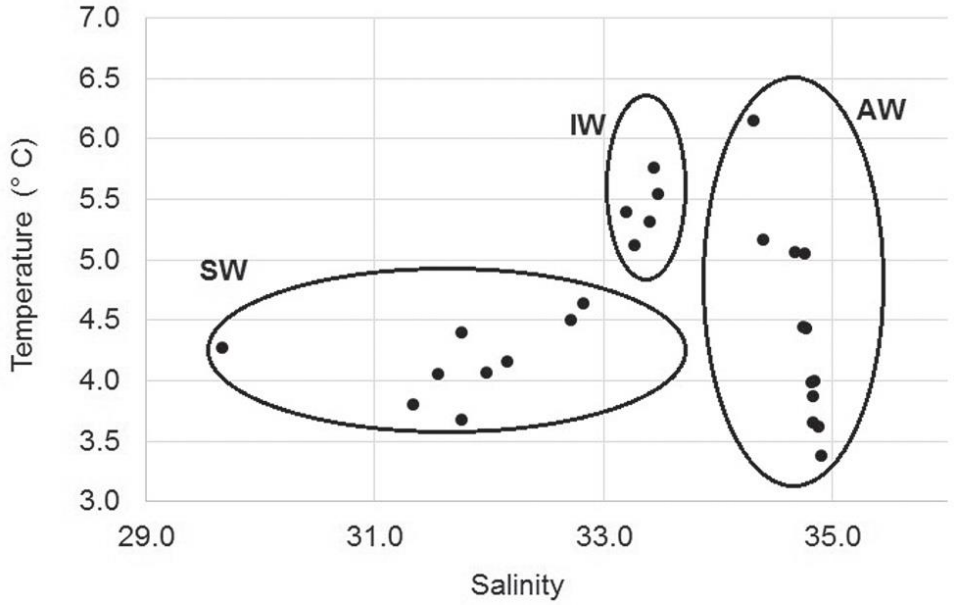


Fig. 3. Distribution of salinity and temperature at the sampling stations of the Kongsfjorden at six depths (surface, 5, 25, 50, 75 and 100 m).

TSM concentrations (range: 1.21-3.11 g m–3) usually decreased from the surface to the 50 m layer, then increased down to the bottom. As already observed for $N\text{-}NO_3^-$, also TSM reached its highest value the second sampling day (MD06).

Nutrient concentrations and N:P ratio measured at the stations 23, 72, 26 and 62 were similar to the values observed at the surface in the MDI station on 6th September. Also TSM concentrations were similar to that observed at the MDI station, except for the station 62 where the highest value of 5.1 mg l^{-1} was measured.

Nutrients were correlated to the thermo-haline features of the column water. Particularly, $N\text{-}NO_2^-$ (–0.42, $p < 0.05$) and $N\text{-}NO_3^-$ (–0.61, $p < 0.01$) were significantly correlated to temperature while $N\text{-}NO_3^-$ (0.40, $p < 0.05$) and $P\text{-}PO_4^{3-}$ (0.76, $p < 10–4$) to salinity. Moreover $N\text{-}NH_4^+$ (0.84, $p < 10–4$) and $N\text{-}NO_3^-$ (0.43, $p < 0.05$) were correlated to N:P. $P\text{-}PO_4^{3-}$was further correlated with $N\text{-}NO_3^-$ (0.58, $p < 0.01$). As concerning TSM amount, it was negatively correlated to salinity ($r = –0.70$, $p < 10–4$) and to $P\text{-}PO_4^{3-}$ concentrations ($r = –0.45$, $p < 0.05$).

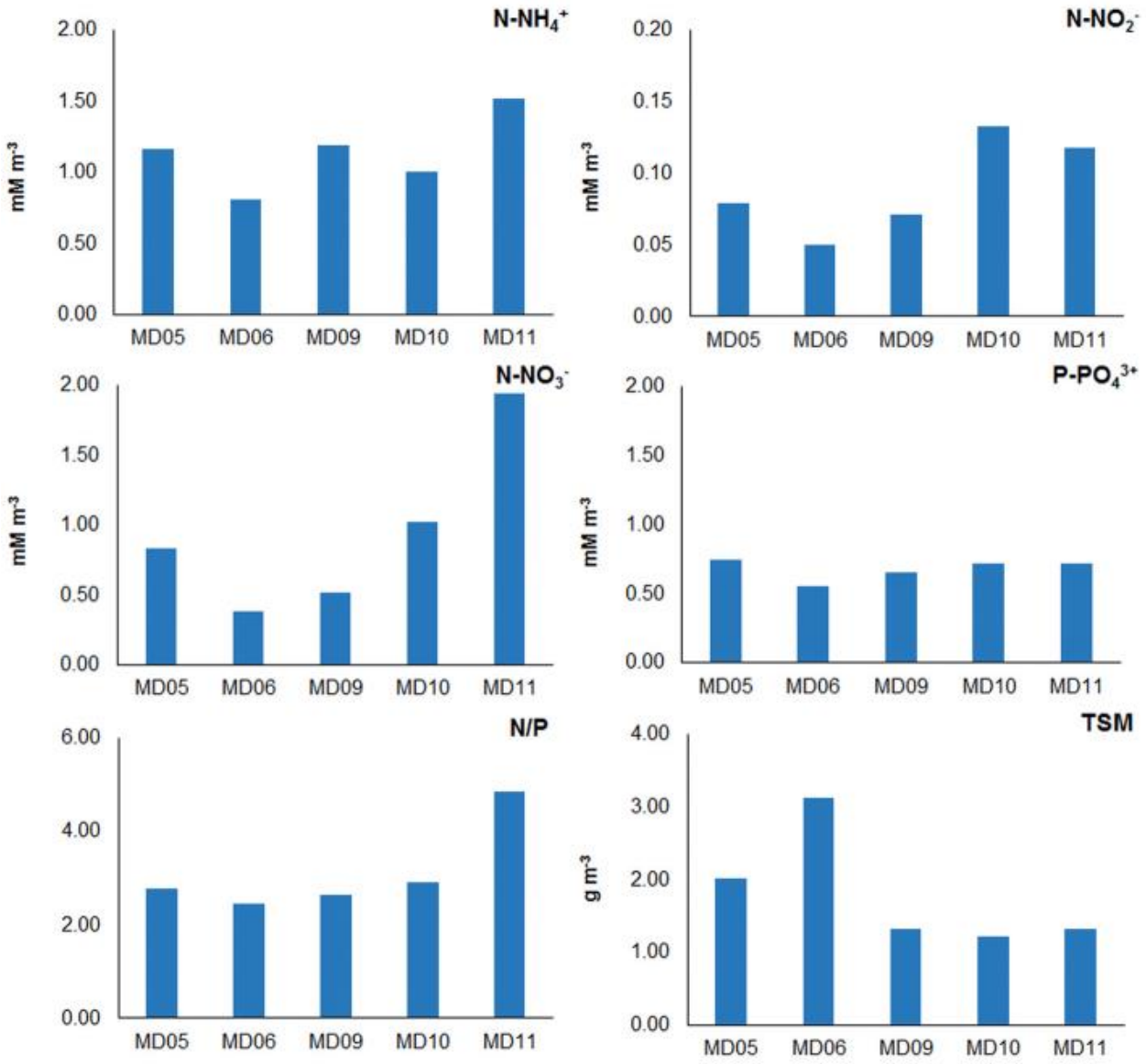


Fig. 4. Weighted mean concentrations of nutrients (mM m^{-3}), N:P ratio and TSM (Total Suspended Matter) (g m^{-3}).

Phytoplankton abundance and biomass

In Figs 5 and 6 the abundance and biomass values of phytoplankton detected at the MDI (MD05, MD06, MD09, MD10, MD11) and other stations (23, 72, 26 and 62) are shown.

The phytoplankton abundances and biomass displayed high variability, ranging from 9.5×10^3 cells l^{-1} to 6.7×10^6 cells l^{-1} and from 0.63 µg C l^{-1} to 5.55 mg C l^{-1}, respectively. During the sampling period, phytoplankton concentrations and biomass values were not particularly high, except for the accumulation/bloom phenomenon, which characterized the time-series MDI station. A total of 76

taxa corresponding to 19 diatoms, 52 dinoflagellates, 2 coccolithophorids, and 3 phytoflagellates were identified (Table 2).

The community was dominated by dinoflagellates in terms of abundance and biomass, which varied from 1.0×10^3 cells l^{-1} to 4.4×10^6 cells l^{-1} and from 0.1 µg C l^{-1} to 5.50 mg C l^{-1}, respectively (Figs 5 and 6). Their percentage contribution to total community ranged from 0.7% to 98.6% (MD10, surface) of the abundances and from 1.4% to 99.9% (MD10, surface) of the biomass. Besides *Prorocentrum* cf. gracile, a high number of other dinoflagellates was detected.

Phytoflagellates were observed throughout the sampling period at all the investigated stations and depths with abundance and biomass values ranging from 7.5 to 686.3×10^3 cells l^{-1} and from 0.2 to 17.1 µg C l^{-1}, respectively. On average they accounted for 26.0 ± 11.6% of total abundance and 0.9 ± 0.3% of total carbon. As a qualitative point of view, phytoflagellates were mainly represented by small forms of uncertain taxonomic identification < 10 µm, and by chryptophyceans and euglenophyceans.

Coccolithophorids were detected with values ranging from 0.04 to 132.9×10^3 cells l^{-1} and from 0.01 to 8.8 µg C l^{-1}, as abundance and carbon content, representing an average of 3.2 ± 1.9% of total abundance and 0.3 ± 0.2% of total carbon, respectively.

Diatoms, when detected, reached the highest concentration (4.5×10^3 cells l^{-1}) and biomass (6.7 µg C l^{-1}) at the station 62. They accounted on average for 0.2 ± 0.1% of the total abundance and biomass.

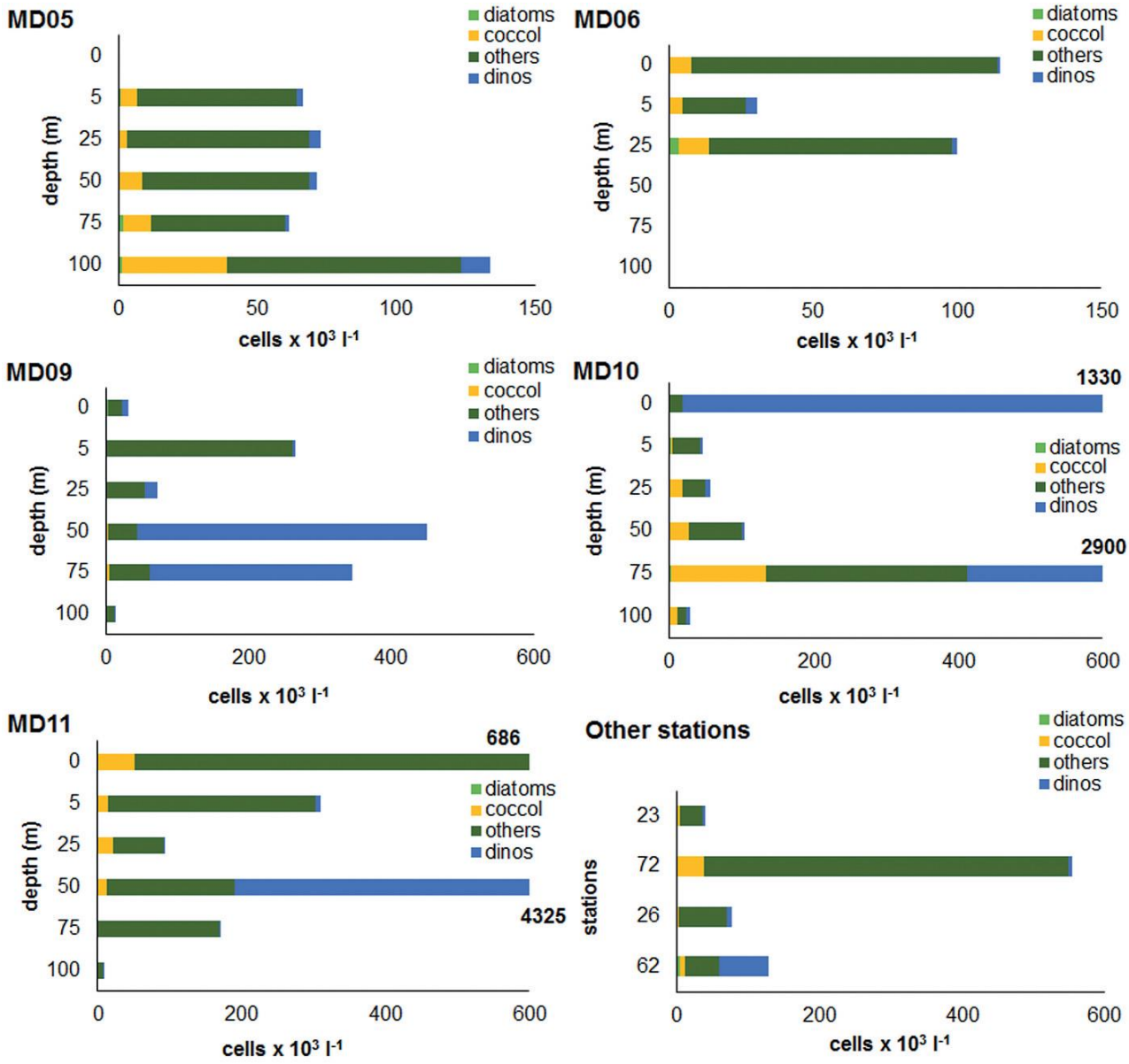


Fig 5. Abundance (cells × 10^3 l^{-1}) of different phytoplankton groups at the sampling stations of the Kongsfjorden.

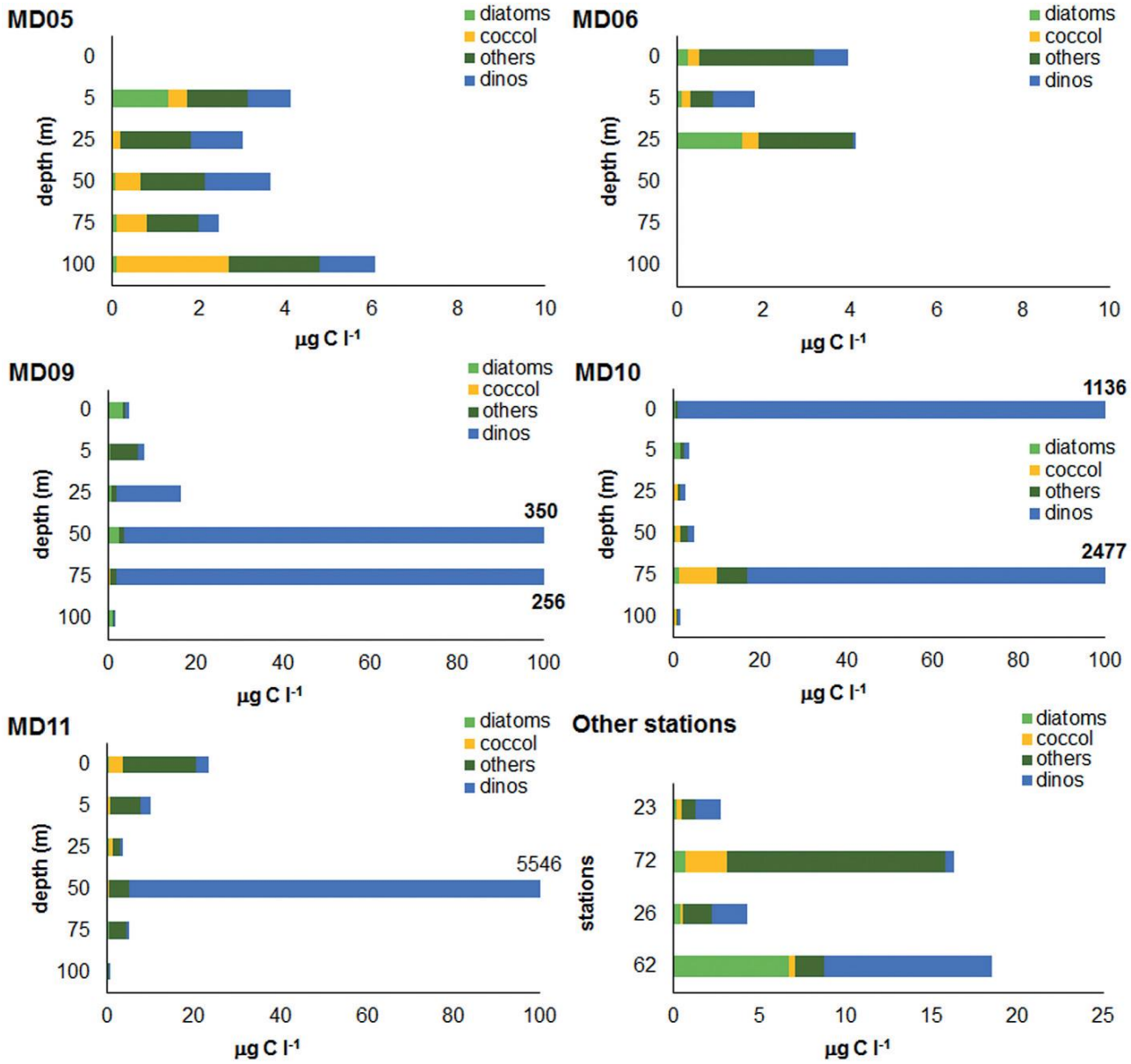
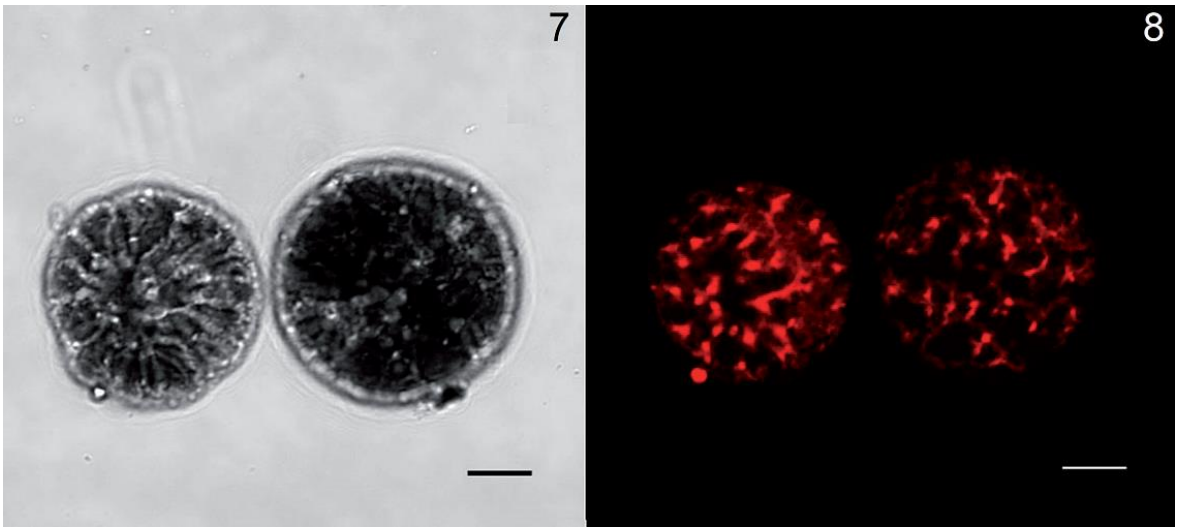


Fig 6. Biomass (µg C l^{-1}) of different phytoplankton groups at the sampling stations of the Kongsfjorden.

Table 2. Occurrence data (minimum, maximum and percentage of presence in the examined samples) of the taxa detected in the Kongsfjorden in September 2013 and comparison with other surveys. References. a = Hasle & Heimdal, 1998; b = Wiktor & Wojciechowska, 2005; c = Seuthe et al., 2011; d = Kubiszyn et al., 2014. Note that in c the comparison have been done only for dinoflagellates

	Min cells l^{-1}	*Max cells l^{-1}*	*Presences %*	*a*	*b*	*c*	*d*
Bacillariophyceae							
Amphora sp.	40	120	13.3				
Cerataulina pelagica (Cleve) Hendey	40	40	3.3				
Chaetoceros decipiens Cleve	80	120	3.3	+	+		
Chaetoceros spp.	40	240	10.0	+			
Cylindrotheca closterium (Ehrenberg) Reimann & J.C. Lewin	40	200	26.7	+	+		
Cocconeis scutellum Ehrenberg	40	80	6.7	+			
Cocconeis sp.	120	240	6.7				
Dactyliosolen fragilissimus (Bergon) Hasle	40	160	16.7				
Grammatophora sp.	160	160	3.3				
Leptocylindrus sp.	360	360	3.3				
Licmophora gracilis (Ehrenberg) Grunow	40	480	13.3				
Licmophora sp.	40	160	20.0				
Navicula spp.	40	1458	30.0	+	+		
Proboscia alata (Brightwell) Sundström	200	200	3.3		+		
Pseudo-nitzschia delicatissima group	40	1480	43.3	+	+		+
Pseudo-nitzschia sp.	80	80	3.3				
Thalassiothrix longissima Cleve & Grunow	120	840	6.7	+			
Thalassiosira gravida Cleve	40	160	3.3	+	+		
Thalassiosira spp.	160	2916	6.7		+		+
Undetermined centric diatoms	40	4374	56.7				
Undetermined pennate diatoms	40	1458	60.0				
Dinophyceae							
Alexandrium sp.	40	4374	36.7			+	
Alexandrium minutum Halim	80	1807920	10.0			+	
Alexandrium cf. *tamarense* (Lebour) Balech	40	120	6.7				
Amphidinium acutissimum Schiller	40	40	3.3				
Amphidinium carterae Hulburt	40	80	16.7		+		
Amphidinium cf. *globosum* Schröder	80	80	3.3				
Amphidinium cf. *latum* Lebour	40	40	3.3				
Amphidinium sphenoides WüIff	80	80	3.3		+	+	
Amphidinium sp.	40	320	33.3	+	+		
Ceratium horridum var. *buceros* (Zacharias) Sournia	40	40	3.3				
Dinophysis acuminata Claparède & Lachmann	40	240	36.7	+		+	
Dinophysis sp.	40	40	3.3			+	
Diplopelta pusilla Balech & R.Akselman	80	120	10.0				
Diplopsalis group	80	80	3.3				
Gymnodinium cf. *pulchellum* J. Larsen	40	120	30.0		+		
Gymnodinium simplex (Lohmann) Kofoid & Swezy	40	1458	30.0		+	+	
Gymnodinium spp.	40	2916	86.7	+	+	+	+
Gyrodinium crassum (Pouchet) Kofoid & Swezy	80	80	3.3				
Gyrodinium fusiforme Kofoid & Swezy	40	80	16.7		+	+	+
Gyrodinium glaucum (Lebour) Kofoid & Swezy	40	160	13.3			+	

	Min cells l⁻¹	*Max cells l⁻¹*	*Presences %*	*a*	*b*	*c*	*d*
Dinophyceae							
Gyrodinium pingue (Schütt) Kofoid & Swezy	40	40	3.3			+	
Gyrodinium spp.	40	1458	43.3	+			
Glenodinium foliaceum F. Stein	40	120	13.3				
Gonyaulax spinifera (Claparède & Lachmann) Diesing	40	40	3.3	+			
Gonyaulax sp.	40	1458	23.3				
Heterocapsa niei (Loeblich III) Morrill & Loeblich III	40	1458	26.7				
Heterocapsa triquetra (Ehrenberg) Stein	40	160	26.7			+	
Katodinium glaucum (Lebour) Loeblich III	40	120	10.0			+	
Lingulodinium polyedrum (Stein) Dodge	40	40	3.3				
Oxytoxum minutum Rampi	1458	1458	3.3				
Oxytoxum parvum Schiller	80	80	6.7				
Oxytoxum rampii Sournia	40	80	10.0				
Oxytoxum variabilis Schiller	40	80	6.7				
Oxytoxum sp.	40	200	16.7				
Phalacroma rotundatum (Claparéde & Lachmann) Kofoid & Michener	40	80	3.3	+	+		
Pronoctiluca pelagica Fabre-Domergue	40	240	23.3		+	+	+
Prorocentrum compressum (Bailey) Abé *ex* Dodge	40	80	6.7				
Prorocentrum cordatum (Ostenfeld) J.D. Dodge	40	320	46.7				
Prorocentrum cf. *gracile* Schütt	80	4723920	33.3				
Prorocentrum cf. *lima* (Ehrenberg) F. Stein	40	40	6.7				
Prorocentrum micans Ehrenberg	40	31401	16.7				
Prorocentrum triestinum J. Schiller	120	120	3.3				
Prorocentrum sp.	40	320	33.3				
Protoperidinium bipes (Paulsen) Balech	40	80	6.7	+	+	+	
Protoperidinium brevipes (Paulsen) Balech	40	40	3.3	+	+	+	
Protoperidinium sp.	40	480	46.7		+	+	
Scrippsiella trochoidea (Stein) Loeblich	80	1458	23.3		+	+	
Scrippsiella like	80	160	10.0				
Torodinium teredo (Pouchet) Kofoid & Swezy	40	40	3.3			+	
Tripos fusus (Ehrenberg) F. Gómez	40	160	10.0				
Tripos longipes (J.W. Bailey) F. Gómez	40	40	3.3				
Tripos macroceros (Ehrenberg) F. Gómez	40	40	3.3			+	
Undetermined naked dinoflagellates	80	46656	83.3				
Undetermined tecate dinoflagellates	80	17496	90.0				
Prymnesiophyceae							
Emiliania huxleyi (Lohmann) Hay *et* Mohler	729	17496	40.0				
Syracosphaera pulchra Lohmann	40	80	10.0				
Undetermined coccolithophorids	40	125604	80.0				
Others							
Eutreptiella sp.	40	80	3.3		+		
Tetraselmis sp.	200	7290	6.7				
Dictyocha speculum Ehrenberg	40	80	3.3	+	+		
Undetermined cryptophyceans	40	2916	16.7				
Undetermined euglenophyceans	1458	5832	6.7				
Undetermined phytoflagellates	7530	686126	100.0				



Figs 7-8. Optical (7) and confocal (8) images of athecate dead dinoflagellates.
Scale = 10 µm.

The temporal distribution showed the dominance of phytoflagellates (up to 83% of the total abundance and 50% of biomass) during the first two days of sampling. Successively, the importance of dinoflagellates increased (up to 40% of the total abundances and 58% of biomass), but phytoflagellates remained an important component of the community. A gradual increase in the number of species (mainly of dinoflagellates) was detected, too.

Moreover, at the surface layer of the stations MDI (MD09 and MD10) and 62, a high number (up to 3.0×10^6 cells l^{-1}) of dead athecate dinoflagellates and/or pellicle cysts (Figs 7-8) was observed.

The correlation analyses evidenced significant relationships of diatoms abundances (–0.41, $p < 0.05$), dinoflagellate abundances (0.47, $p < 0.05$) and biomass (0.44, $p < 0.05$), phytoplankton abundances (0.55, $p < 0.01$) and biomass (0.49, $p < 0.05$) with TSM. Moreover, coccolithophorid abundances (–0.47, $p < 0.05$) and biomass (0.42, $p < 0.05$) showed significant correlations with N-NO_3^- and salinity, respectively.

Dynamics and morphology of dinoflagellates forming bloom

During the first two days of sampling at the MDI station (MD5 and MD6), phytoplankton abundance and biomass did not exceed the cell concentrations of 140×10^3 cells l^{-1} and 4.1 µg C l^{-1} (Figs 5 and 6). The third day (MD09), an increase of the dinoflagellate *Prorocentrum* cf. *gracile* abundance and biomass was observed at the depths of 50 m (451.0×10^3 cells l^{-1}, 354 µg C l^{-1}) and 75 m (346.5×10^3 cells l^{-1}, 258.0 µg C l^{-1}). The first microalgal accumulation (Fig. 9) was detected the fourth day of sampling (MD10), when a bloom, due mainly to the dinoflagellate *Prorocentrum* cf. *gracile* was

observed at the surface layer (1.3×10^6 cells l^{-1}, 1.1 mg C l^{-1}) and at the 75 m layer (2.9×10^6 cells l^{-1}, 2.5 mg C l^{-1}).

During the fifth day (MD11) *Prorocentrum* cf. *gracile* together with *Alexandrium minutum* peaked at the 50 m layer with values of 4.7×10^6 cells l^{-1} and 3.9 mg C l^{-1} and 1.8×10^6 cells l^{-1} and 1.6 mg C l^{-1}, respectively.

Prorocentrum cf. *gracile* cells were small-sized, elongate and lanceolate; they were more than twice as long as broad (Figs 10-12). The anterior end was rounded and the posterior end pointed. There was an anterior long spine. Poroids were distributed all over the thecae (Fig. 12). Length (l): 32.6 ± 3.9 µm, width (w): 13.6 ± 2.7 µm, l/w: 2.0 ± 0.4 length of spine: 7.6 ± 1.6 µm, n = 50.

Cells of *Alexandrium minutum* were small, nearly spherical to ellipsoidal (Fig. 13) and measured 26.5 ± 2.4 µm and 24.8 ± 2.2 µm in width (n = 30). The plates were fine and smooth, and the tabulation was typical for *Alexandrium*.

The apical pore complex (APC) was oval and pointed posteriorly (Figs 14-15). The apical pore plate (Po) was large, narrow and oval and was in direct contact with the first apical plate (1'), which was typically slender and rhomboidal (Fig. 14). The characteristic ventral pore was no detected in the specimens examined. The sixth precingular plate (6'') was long and narrow (Fig.14). The anterior sulcal plate was usually wider than long (Fig. 16). Epithecal profile was conical with convex sides. The apex was rounded. The hypotheca was hemielliptical with a flat antapex (Fig. 16). The deeply excavated cingulum showed a descending mode (Fig. 16)

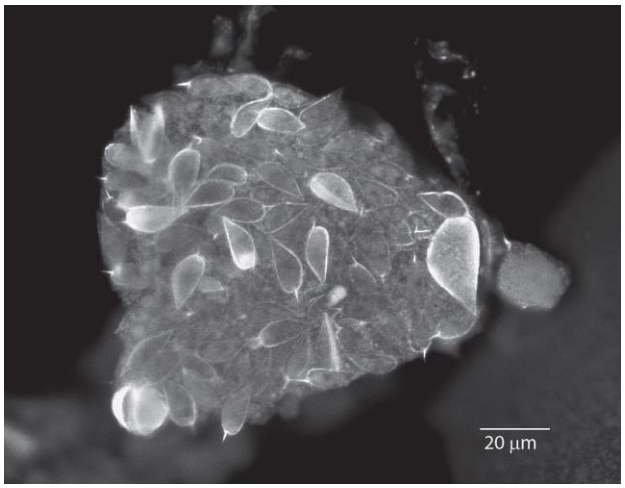
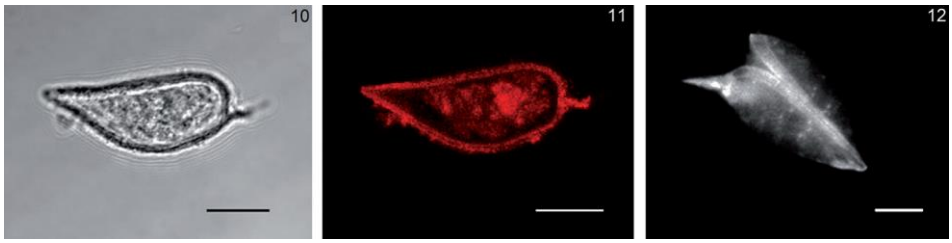
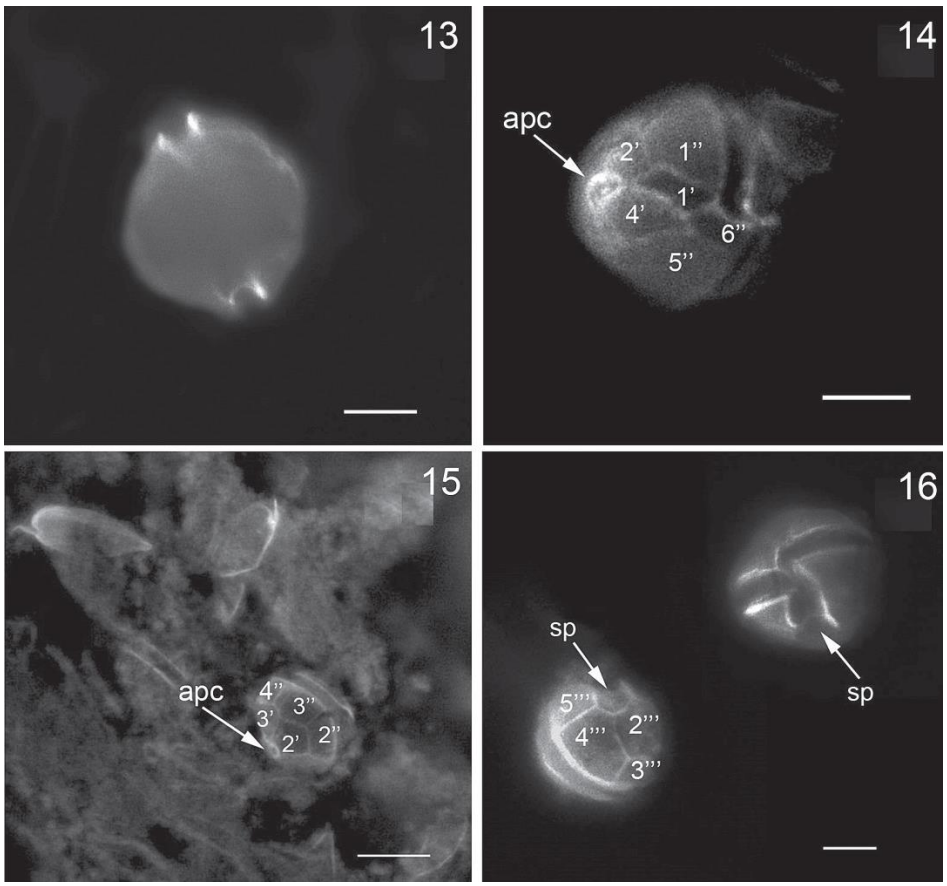


Fig. 9. Cell aggregates stained by Calcofluor and analyzed by epifluorescence microscopy. Scale = 20 µm



Figs 10-12. Optical (10), confocal (11) and epifluorescent (12) images of *Prorocentrum* cf. *gracile*. Scale = 10 µm.



Figs 13-16. *Alexandrium minutum* stained by Calcofluor and analyzed by epifluorescence microscopy. 13. General view; 14. ventral view; 15. dorsal view (scale = 20 µm); 16. Antapical view, with the "sulcal plate". Scale = 10 µm.

DISCUSSION

Environmental data and relationships with phytoplankton

The studies carried out at the coastal stations of the Kongsfjorden confirmed the influence of the inflow of Atlantic water from the open ocean as well as the freshwater runoff of the melting glaciers on the biological features of the fjord (Keck et al., 1999; Wiktor & Wojciechowska, 2005; Azzaro et al., 2014; Kubiszyn et al.,

2014). Our data evidenced the presence of three water masses with different termohaline characteristics: a low-salinity surface layer derived from melting glaciers and rivers (up to 25m) (SW), a deeper layer (between 75 and 100m) with more saline AW and IW localized at the depth of 50 m, according to the classification proposed by Cottier et al. (2005).

As concerning nutrient concentrations previously observed in summer, data collected in the outer part of Kongsfjorden (as means for the upper 20 m) evidenced nitrate (1.6-3.3 µM) and phosphate concentrations (0.5 µM), respectively higher than (0.6-1.1 µM) and close (0.5-0.7 µM) to our estimates, respectively (Hop et al., 2002). Irversen & Seuthe (2011) reported at the upper 50 m (September 2006) of a station close to the Kongsfjorden, a mean value of nitrate and phosphate, respectively double and three times lower than our data. Consequently, the N:P ratio was higher in September 2006 (6.2), compared to the values determined during this study.

Moreover, a large percentage of nitrogen was available in the form of ammonium and at the surface layer, this nutrient reached its highest concentrations and temporal variability. Presumably, nutrient dynamics was related to the thermohaline features of the column water, as evidenced by the relationships between the hydrological characteristics and nutrients, and particularly nitrate.

The analysis of long-term precipitation trends from the Svalbard region indicated an intensification of annual precipitation during the last 20 years resulting in an increase of the meltwater input (Førland et al., 2011). Consequently, recent climate changes were responsible for the enhancement of the total suspended matter (TSM) load entering the fjord (Zaborska et al., 2006). During our investigation it was raining in the fjord and a high concentration of TSM was detected. These amounts reflected the runoff of glaciers (as confirmed by the correlation analysis), which brings meltwater and particles into the fjord (Beszczyńska−Møller et al., 1997).

Our findings did not evidence any significant effect of inorganic nutrients on phytoplankton, but on the contrary melting freshwaters, associated to high amounts of TSM, affected these planktonic components, and particularly the dinoflagellate dynamics and biomass, as resulted by statistical analyses.

Phytoplankton assemblages

Phytoplankton abundance and biomass monitored during this survey were higher than the previously collected data in the Kongsfjorden (Hop et al., 2002; Seute et al., 2011; Kubiszyn et al., 2014; Bhaskar et al., 2016). Particularly, responsible for the increase of abundance and biomass values was a dinoflagellate bloom/aggregation observed since the third sampling day.

Previous studies indicated that in summer, diatoms were the most important components of the phytoplankton communities in the fjord (Hop et al., 2002). More recent data suggested an increased importance of flagellates, probably related to the increased inflow of the warm AW in the Kongsfjorden (Piwosz et al., 2009; Kubiszyn et al., 2014). Warming and stability of the water column favour rather flagellates than diatoms, which develop in mixed waters. Kubiszyn & coauthors (2014) monitored the dominance of nanoplanktonic autotrophs (cryptophytes) and microplanktonic heterotrophic protist (dinoflagellates and ciliates) in the fjord during their three surveys carried out in summer in the West Spitsbergen area. More recent researches demonstrated both the dominance of prymnesiophytes and raphidophytes in surface waters and the heterotrophic dinoflagellates (the major contributors to phytoplankton biomass) throughout all the column water (Bhaskar et al., 2016).

Our study confirmed these findings because diatoms were represented by low cell numbers and biomass, and by few species, like cosmopolitan (*Cerataulina pelagica, Chaetoceros decipiens, Cylindrotheca closterium, Thalassiosira gravida, Pseudo-nitzschia delicatissima* group) and cold water taxa (*Thalassiothrix longissima*).

During the first two days of sampling, nano-sized phytoflagellates and coccolithophorids (*Emiliania huxleyi* and *Syracosphaera pulchra*), both indicators of the Atlantic inflow (Hop et al., 2002; Hegseth & Sundfjord, 2008) dominated the phytoplankton community. The haptophycean Phaeocystis pouchetii, detected in previous studies (Hop et al., 2002; Wiktor & Wojciechowska, 2005; Kubiszyn et al., 2014) seemed to be absent in our samples. However, by considering the high number of phytoflagellates of uncertain taxonomical identification, the presence of this species cannot be excluded.

The physiognomy of phytoplankton assemblages changed dramatically during the following days, probably related to the hydrological regime, and an increase of abundance, biomass and species number (mainly dinoflagellates) was detected. Dinoflagellates were mainly represented by species typical of estuarine and coastal cosmopolitan environments, such as *Alexandrium minutum, A. tamarense.* *Scrippsiella trochoidea, Gonyaulax spinifera, Prorocentrum micans* and *P. cordatum.* Moreover, species representative of temperate and warm waters were also identified: *Amphidinium carterae, Gyrodinium pingue, Heterocapsa niei, H. triquetra, Katodinium glaucum* and *Torodinium teredo*. Among the observed taxa, several are known to be harmful; they comprised diatoms (*Pseudo-nitzschia delicatissima* group) and dinoflagellates (*Alexandrium minutum, A. tamarense, Dinophysis acuminata, Dinophysis* sp.*, Gonyaulax spinifera, Phalacroma rotundatum*). The presence of harmful species has been already evidenced in other studies carried out in the main coastal circumarctic regions (Poulin et al., 2011). Our data showed that these species are extending their distribution also in the Kongsfjorden where cosmopolitan (*A. tamarense, Prorocentrum cordatum*) and temperate-warm waters harmful species (*Amphidinium carterae, Lingulodinium polyedrum, Prorocentrum* cf. *lima*) were identified for the first time.

Hallegraeff (2010) suggested that variations in phytoplankton physiognomy provide a sensitive early warning for climate-driven perturbations to marine ecosystems and particularly indicated some effects related to global warming. Among these effects, the expansion range of warm-water species at expense of coldwater species, and the increase in the abundance of harmful taxa are presumed. According to Hallegraeff (2010), some harmful species (e.g. toxic dinoflagellates benefiting from land runoff and⁄or water column stratification) may increase their presence, while others decrease in the impacted areas.

Dinoflagellate aggregation

Living, senescent and dead algae, mainly diatoms compose macroaggregates, which are also constituted by phytodetritus, bacteria, protozoans, zooplankton, fecal pellets, macrophyte detritus, clay and silt minerals, calcite and other particles scavenged from the surrounding water (Simon et al., 2002 and references herein). As concerning dinoflagellates, there are few recorded instances of these microalgae

being associated with pelagic aggregates (California, Alldredge et al., 1998; Tasman Bay, New zealand: MacKenzie et al., 2002). In these cases, the involved species belonged to Gonyaulax genera. Experimental work on cultures of Gonyaulax hyalina (Ostenfeld et Schmidt) carried out by MacKenzie et al. (2002) revealed the capacity of this dinoflagellate to produce transparent exo-polymers (TEPs), which hitherto were known as a product of diatoms and bacteria (Simon et al., 2002).

The phenomenon of algal aggregation is common and important in the Arctic Ocean where ice algae represent a second source of primary production. Ice algae are released in spring and summer as a consequence of the ice melt, and are mainly represented by diatoms (Lee et al., 2011; Fernández-Méndez et al., 2014). Diatom aggregates sink and reach the seafloor (Boetius et al., 2013) or remain suspended in the water column through the production of oxygen trapped in the aggregates (Fernández-Méndez et al., 2014). Increasing extent of annually formed sea ice over the Arctic Ocean is resulting in higher biomass of sympagic (i.e., seaice-associated) unicellular eukaryotes available for the upper trophic levels (Fernández-Méndez et al., 2014). Macro-aggregate accumulation of dinoflagellates occurring in the coastal waters of the Kongsfjorden is a new phenomenon in the Arctic waters that differs from the dinoflagellate accumulation observed in other sites. Algal aggregation appeared to be associated to the mobilization of mineral suspensoids (the so-called "glacial flour", Sommaruga, 2015) and not to the production of TEPs. Presumably in this case, the large amount of different inorganic (Hodson, 2006) and organic molecules in the form of dissolved and particulate carbon) (Hood et al., 2009; 2015), associated to the glacial flour and buried under the ice, could have represented an efficient source readily available to the mixotrophic dinoflagellates *Prorocentrum* cf. *gracile* and *Alexandrium minutum* (Jeong et al., 2010). These dinoflagellates could have found favourable conditions to their growth and bloomed at the surface and in deep waters. Likely, aggregation of dinoflagellates with glacial flour might: i) result in more rapid transport of dinoflagellate-generated material to the deep ocean, ii) alter the nature of sinking particulate matter; iii) increase the nutritional value of glacial flour as a food source for zooplankton and fish (Alldredge et al., 1998).

Recently, Sommaruga (2015) suggested the necessity to deepen the knowledge on the ecology of turbid glacier-fed aquatic ecosystems, and particularly on the effects of glacial flour on planktonic organisms. Some studies carried out in turbid glacial-fed lakes, revealed that microbes dominated food webs, while autotrophic microorganisms and heterotrophic nanoflagellates were present at low abundance probably for the negative effects of turbidity (Sommaruga & Kandolf, 2014). In such ecosystems and in coastal waters, mixotrophic phytoplankton could apparently represent the trophic link to bacteria, because the combination of photosynthesis and phagotrophy benefits them despite the negative influence of the glacial flour and turbidity (Sommaruga, 2015). In theory, this could be the case of dinoflagellate aggregation in Kongsfjorden.

Finally, *Prorocentrum gracile* is a neritic species and cosmopolitan in cold temperate to tropical waters (Steidinger & Tangen, 1996). The morphology of our specimens was characterized by a smaller size than those described by Cohen-Fernandez & coauthors (2006) and further electronic microscopy and molecular analyses should be done to confirm the identity of the species detected during our investigation. If these analyses give a positive response, our study represent the first evidence of the presence of *Prorocentrum gracile* in the Arctic waters.

Alexandrium minutum is a widely distributed species found in many coastal areas of the world, and it has been already detected by Seuthe et al. (2011) in Kongsfjorden. This dinoflagellate is a harmful species producing paralytic shellfish poisoning toxins and dense reddish-brown tides in coastal waters throughout the world (Anderson, 1998; Anderson et al., 2012).

In conclusion, the ecological succession of phytoplankton reflects the hydrological conditions of the Kongsfjorden fjord, characterized in the first days of monitoring by the dominance of the Atlantic inflow and later by the input of sediment-rich glacial meltwaters. These conditions affected dramatically the phytoplankton physiognomy both in terms of biomass and species composition. Turbid waters favour mixotrophic species, which gave rise to dinoflagellate aggregations, monitored for the first time in the Arctic. Moreover, the phytoplankton assemblages were characterized by the increased presence of temperate-warm species, including harmful and toxic species. Both these evidences support the

urgency to increase our knowledge of the biodiversity of these communities, which represent an excellent sentinel of the changes in the Arctic coastal systems. These findings, even if preliminary, suggest also the necessity to study how changes in phytoplankton physiognomy and additional pulses of biomass may alter the food web structure and the biogeochemical cycles.

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REFERENCES

ALLDREDGE A.L., PASSOW U. & HADDOCK S.H.D., 1998 — The characteristics and transparent exo-polymer (TEP) particle content of marine snow formed from thecate dinoflagellates. Journal of plankton research 20: 393-406.

AMINOT A. & CHAUSSEPIED M., 1983 — Manuel des analyses chimiques en milieu marin. CNEXO (Centre National pour l'Exploration des Océans), Brest, 395 p.

ANDERSON D.M., 1998 — Physiology and bloom dynamics of toxic Alexandrium species, with emphasis on life cycle transition. In: Anderson D.M., Cembella A.D. & Hallegraeff G.M. (eds), The Physiological Ecology of Harmful Algal Blooms. Heidelberg, Springer-Verlag, pp. 29-48.

ANDERSON D.M., ALPERMANN T.J., CEMBELLA A.D., COLLOS Y., MASSERET E. & MONTRESOR M., 2012 — The globally distributed genus Alexandrium: multifaceted roles in marine ecosystems and impacts on human health. Harmful algae 14: 10-35. doi:10.1016/j. hal.2011.10.012.

ARRIGO K.R. & VAN DIJKEN G.L., 2015 — Continued increases in Arctic Ocean primary production. Progress in oceanography 136: 60-70.

AZZARO M., LA FERLA R., MAIMONE G., AZZARO F., DECEMBRINI F., CAROPPO C., LANGONE L., GIGLIO F, MISEROCCHI S. & ALIANI S., 2014 — Dynamics of microbial biomass and respiratory activity during late summer in a site of Arctic Kongsfjorden. Front. Mar. Sci. Conference Abstract: IMMR | International Meeting on Marine Research 2014. doi: 10.3389/conf.FMARS.2014.02.00132.

BHASKAR J.T., TRIPATHY S.C., SABU P., LALURAJ C.M. & RAJAN S., 2016 — Variation of phytoplankton assemblages of Kongsfjorden in early autumn 2012: a microscopic and pigment ratio-based assessment. Environmental monitoring assessment 188(4): 224.

BESZCZYŃSKA-MÖLLER A., WĘSŁAWSKI J.M., WALCZOWSKI W. & ZAJĄCzKOWSKI M., 1997 — Estimation of glacial meltwater discharge into Svalbard coastal waters. Oceanologia 39: 289-298.

BOETIUS A., ALBRECHT S., BAKKER K., BIENHOLD C., FELDEN J., FERNANDEZ-MÉNDEZ M., HENDRICKS S., KATLEIN C., LALANDE C., KRUMPEN T., NICOLAUS M., PEEKEN I., RABE B., ROGACHEVA A., RYBAKOVA E., SOMAVILLA CABRILLO R. & WENZHÖFER F., 2013 — Export of algal biomass from the melting Arctic sea ice. Science 339: 1430-1432. doi:10.1126/science.1231346.

COHEN-FERNANDEZ E.J., DEL CASTILLO E.M., SALGADO UGARTE I.H. & PEDROCHE F.F., 2006 — Contribution of external morphology in solving a species complex: The case of *Prorocentrum micans*, *Prorocentrum gracile* and *Prorocentrum sigmoides* (Dinoflagellata) from the Mexican Pacific Coast. Phycological research 54: 330-340.

COTTIER F., TVERBERG V., INALL M., SVENDSEN H., NILSEN F. & GRIFFITH C., 2005 — Water mass modification in an Arctic fjord through cross-shelf exchange: The seasonal hydrography of Kongsfjorden, Svalbard. Journal of geophysical research (Oceans) 110. doi: 10.1029/2004JC00275.

EILERTSEN H.C., TAASEN J.P. & WESLAWSKI J.M., 1989 — Phytoplankton studies in the fjords of West Spitzbergen: physical environment and production in spring and summer. Journal of plankton research 11(6): 1245-1260.

FERNANDEZ-MÉNDEZ M., WENZHÖFER F., PEEKEN I., SØRENSEN H.L., GLUD R.N. & BOETIUS A., 2014 — Composition, Buoyancy Regulation and Fate of Ice Algal

Aggregates in the Central Arctic Ocean. PLoS ONE 9 (9): e107452. doi:10.1371/journal.pone.0107452.

FØRLAND E.J., BENESTAD R., HANSSEN-BAUER I., HAUGEN J.E. & SKAUGEN T.E., 2011 —Temperature and Precipitation Development at Svalbard 1900-2100. Advances in meteorology 2011: 1-14.

FRITZ L. & TRIEMER R.E., 1985 — A rapid simple technique utilizing Calcofluor White M2R for the visualization of dinoflagellate thecal plates. Journal of phycology 21: 662-664.

HALLDAL P. & HALLDAL K., 1973 — Phytoplankton, chlorophyll, and submarine light conditions in Kings Bay, Spitsbergen, July 1971. Norwegian journal of botany 20: 99-108.

HALLEGRAEFF G.M, 2010 — Ocean climate change, phytoplankton community responses, and harmful algal blooms: a formidable predictive challenge. Journal of phycology 46: 220-235.

HASLE G.R. & VON QUILLFELDT C.H., 1996 — Part 8. Marine microalgae. In: Elvebakk A. & Prestrud P. (eds), A catalogue of Svalbard plants, fungi, algae and cyanobacteria. Norsk polarinstitutt Skrifter 198: 375-382.

HASLE G.R. & HEIMDAL B.R., 1998 — The net phytoplankton in Kongsfjorden, Svalbard, July 1988, with general remarks on species composition of arctic phytoplankton. Polar research 17(1): 31-52.

HEGSETH E.N. & SUNDFJORD A., 2008 — Intrusion and blooming of Atlantic phytoplankton species in the high Arctic. Journal of marine systems 74: 108-119.

HEGSETH E.N. & TVERBERG V., 2013 — Effect of Atlantic water inflow on timing of the phytoplankton spring bloom in a high Arctic fjord (Kongsfjorden, Svalbard). Journal of marine systems 113-114: 94-105.

HILLEBRAND H., DURSELEN C.D., KIRSCHTEL D., POLLINGHER U. & ZOHARY T., 1999 — Biovolume calculation for pelagic and benthic microalgae. Journal of phycology 35: 403-424.

HODSON A.J., 2006 — Phosphorus in glacial meltwaters, In: Knight P.G. (ed.), Glacier Science and Environmental Change. Blackwell Publication, Malden MA, pp. 81-82.

HOOD E., FELLMAN J., SPENCER R.G.M., HERNES P.J., EDWARDS R., D'AMORE D. & SCOTT D., 2009 — Glaciers as a source of ancient and labile organic matter to the marine environment. Nature 462: 1044-1047.

HOOD E., BATTIN T., FELLMAN J., O'NEEL S. & SPENCER R.G.M., 2015 — Storage and release of organic carbon from glaciers and ice sheets. Nature geoscience 68: 91-96. doi:10.1038/ngeo2331.

HOP H., PEARSON T., HEGSETH E.H., KOVACS K.M., WIENCKE C., KWASNIEWSKI S., EIANE K., MEHLUM F., GULLIKSEN B., WLODARSKA-KOWALCzUK M., LYDERSEN C., WESLAWSKI J.M., COCHRANE S., GABRIELSEN G.W., LEAKEYR.J.G., LØNNE O.J., ZAJACzKOWSKI M., FALK-PETERSEN S., KENDALL M., WÄNGBERG S-A., BISCHOF K., VORONKOV A.Y., KOVALTCHOUK N.A., WIKTOR J., POLTERMANN M., DI PRISCO G., PAPUCCI C. & GERLAND S., 2002 — The marine ecosystem of Kongsfjorden, Svalbard. Polar research 21: 167-208.

IRVERSEN K.R. & SEUTHE L., 2011 — Seasonal microbial processes in a high-latitude fjord (Kongsfjorden, Svalbard): I. Heterotrophic bacteria, picoplankton and nanoflagellates, Polar biology 34: 731-749.

JEONG H.J., YOO Y.D., KIM J.S., SEONG K.A., KANG N.S. & KIM T.H., 2010 — Growth, Feeding and Ecological Roles of the Mixotrophic and Heterotrophic Dinoflagellates in Marine Planktonic Food Webs. Ocean science journal 45(2): 65-91. doi: 10.1007/s12601-010-0007-2.

JI R., EDWARDS M., MACKAS D.L., RUNGE J.A. & THOMAS A.C., 2010 — Marine plankton phenology and life history in a changing climate: current research and future directions. Journal of plankton research 32: 1355-1368.

JI R., JIN M. & VARPE O., 2013 — Sea ice phenology and timing of primary production pulses in the Arctic Ocean. Global change biology 19: 734-741.

KAHRU M., BROTAS V., MANzANO-SARABIA M. & MITCHELL B.G., 2011 — Are phytoplankton blooms occurring earlier in the Arctic? Global change biology 17: 1733-1739.

KECK A., WIKTOR J., HAPTER R. & NILSEN R., 1999 — Phytoplankton assemblages related to physical gradients in an arctic, glacier-fed fjord in summer. ICES journal of marine science, 56: 203-214.

KUBISzYN M., PIWOSz K., WIKTOR J.M. JN & WIKTOR J.M., 2014 — The effect of inter-annual Atlantic water inflow variability on the planktonic protist community structure in the West Spitsbergen waters during the summer. Journal of plankton research 36(5): 1190-1203.

LEE S.H., MCROY C.P., JOO H.M., GRADINGER R., CUI X., YUN M.S., CHUNG K.H., KANG S.-H., KANG C.-K., CHOY E.J., SON S., CARMACK E. & WHITLEDGE T.E., 2011 — Holes in progressively thinning Arctic sea ice lead to new ice algae habitat. Oceanography 24(3): 302-308.

LI W.K.W., MCLAUGHLIN F.A., LOVEJOY C. & CARMACK E.C., 2009 — Smallest Algae Thrive As the Arctic Ocean Freshens. Science 326: 539. doi: 10.1126/science.1179798

MACKENZIE L., SIMS I., BEUzENBERG V. & GILLESPIE P., 2002 — Mass accumulation of mucilage caused by dinoflagellate polysaccharide exudates in Tasman Bay, New zealand. Harmful algae 1: 69-83.

MCLAUGHLIN F.A. & CARMACK E.C., 2010 — Deepening of the nutricline and chlorophyll maximum in the Canada Basin interior, 2003-2009. Geophysical research letters 37: L24602. doi:10.1029/2010GL045459.

MENDEN-DEUER S. & LESSARD E.J., 2000 — Carbon to volume relationships for dinoflagellates, diatoms and other protest plankton. Limnology and oceanography 45(3): 569-579.

PIQUET A.M.-T., SCHEEPENS J.F., BOLHUIS H., WIENCKE C. & BUMAA.G.J., 2010 — Variability of protistan and bacterial communities in two Arctic fjords (Spitsbergen). Polar biology 33: 1521-1536.

PIWOSz K., WALKUSz W., HAPTER R., WIECzOREK P., HOP H. & WIKTOR J., 2009 — Comparison of productivity and phytoplankton in a warm (Kongsfjorden) and a cold (Hornsund) Spitsbergen fjord in mid-summer 2002. Polar biology 32: 549-559.

POULIN M., DAUGBJERG N., GRADINGER R., ILYASH L., RATKOVAT. & VON QUILLFELDT C., 2011 — The pan-Arctic biodiversity of marine pelagic and sea-ice unicellular eukaryotes: a first-attempt assessment. Marine biodiversity 41: 13-28. doi: 10.1007/s12526-010-0058-8.

SEUTHE L., IVERSEN K.R. & NARCy F., 2011 — Microbial processes in a high-latitude fjord (Kongsfjorden, Svalbard): II. Ciliates and dinoflagellates. Polar biology 34: 751-766.

SIMON M., GROSSART H.-P., SCHWEITzER B. & PLOUG H., 2002 — Microbial ecology of organic aggregates in aquatic ecosystems. Aquatic microbial ecology 28: 175-211.

SOMMARUGA R., 2015 — When glaciers and ice sheets melt: consequences for planktonic organisms. Journal of plankton research 37(3): 509-518.

SOMMARUGA R. & KANDOLF G., 2014 — Negative consequences of glacial turbidity for the survival of freshwater planktonic heterotrophic flagellates. Scientific reports 4. doi:10.1038/srep04113.

STEIDINGER K.A. & TANGEN K., 1996 — Dinoflagellates. In: Tomas C.R. (ed.), Identifying Marine Diatoms and Dinoflagellates. New york, Academic Press, pp. 387-598.

STRICKLAND J.D.H. & PARSON T.R., 1972 — A practical handbook of seawater analysis. Bulletin of the fisheries research board of Canada 167: 1-311.

TOTTI C., DE STEFANO M., FACCA C. & GHIRARDELLI L.A., 2004 — Microphytobenthos. In: Gambi, M.C. & Dappiano, M. (eds), Mediterranean Marine Benthos: A Manual of Methods for its sampling and study. Biologia marina Mediterranea 11 (1): 247-266.

UTERMÖHL H., 1958 — zur Vervollkommnung der quantitativen Phytoplankton-Methodik. Mitteilung Internationale Vereinigung fuer Theoretische unde Amgewandte Limnologie 9: 1-38.

WANG G., GUO C., LUO W., CAI M. & HE J., 2009 — The distribution of picoplankton and nanoplankton in Kongsfjorden, Svalbard during late summer 2006. Polar biology 32: 1233-1238.

WASSMANN P., DUARTE C.M., AGUSTÍ S. & SEJR M.K., 2011 — Footprints of climate change in the Arctic marine ecosystem. Global change biology 17: 1235-1249.

WIKTOR J. & WOJCIECHOWSKA K., 2005 — Differences in taxonomic composition of summer phytoplankton in two fjords of West Spitsbergen, Svalbard. Polish polar research 26 (4): 259-268.

ZABORSKA A., PEMPKOWIAK J. & PAPUCCI C., 2006 — Some sediment characteristics and sedimentation rates in an Arctic Fjord (Kongsfjorden, Svalbard). Srodkowo-Pomorskie Towarzystwo Naukowe Ochrony Srodowiska 8: 79-96. http://www.ros.edu.pl/images/roczniki/archive/pp_2006_006.pdf.

ZINGONE A., TOTTI C., SARNO D., CABRINI M., CAROPPO C., GIACOBBE M.G., LUGLIÈ A., NUCCIO C. & SOCAL G., 2010 — Fitoplancton: metodiche di analisi quali-quantitativa. In: Socal G., Buttino I., Cabrini M., Mangoni O., Penna A. & Totti C. (eds), Metodologie di studio del plancton marino, Manuali e Linee Guida 56/2010. Roma, ISPRA SIBM, pp. 213-237.